

THE BIOGEOGRAPHY OF THE DEEP-SEA OCTOPODA

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ABSTRACT

The deep-sea octopods are in both octopod suborders, the Cirrata with three families, eight genera and 29 species, and the Incirrata with three octopodid subfamilies, 11 genera and 48 species. In addition, some families in the Incirrata contain deep-sea pelagic species. Only benthic or "near benthic" species are dealt with in this paper.

Among the Cirrata, only the Cirroteuthidae contain species with a multi-ocean distribution. *Cirrothauma murrayi* is possibly cosmopolitan, occurring from polar seas to the depths of the tropics. *Cirroteuthis muelleri* has an amphiboreal distribution in the North Atlantic and North Pacific. In the monotypic Stauroteuthidae, *Stauroteuthis syrtensis* is known only from the temperate western North Atlantic. The Opisthoteuthidae are represented by two genera. *Opisthoteuthis* with 10 species is the shallowest-dwelling of the cirrates, with all but three species living between 100 and 1000 m. The genus is distributed throughout the oceans except in high latitudes. *Grimpoteuthis*, with 13 species, occurs in all oceans but no species is recorded from more than one ocean. A specimen has been trawled from 7279 m.

The deep-sea Incirrata are found among three subfamilies of the Octopodidae. In the Bathypolypodinae, *Bathypolypus* has five species in the Atlantic, one off Japan, one in the Indian Ocean; *Teretopus* has two species in the Indian Ocean, and *Benthoctopus* has approximately 15 species distributed worldwide from the Antarctic to the Arctic, with individual species restricted to single oceans. Among the Pareledoninae, *Pareledone*, *Vosseledone* and *Velodona* are found only in the southern hemisphere, and *Tetracheledone* only in the western North Atlantic. *Pareledone* is the most speciose and has a circum-Antarctic distribution; the monotypic *Vosseledone* is known only from Brazil; the two species of *Velodona* occur off East Africa. Among the Graneledoninae, *Graneledone* has two species in the Southern Ocean, one in the North Atlantic, one in the North Pacific and one in the Panamic region. *Thaumeledone* and *Bentheledone* are confined to the Southern Ocean.

Key words: biogeography; deep sea; Octopoda; Cirrata; Incirrata.

INTRODUCTION

The deep-sea octopods (defined as those octopods that live below the edge of the continental shelf) are in both suborders, the Cirrata and the Incirrata. The cirrates, or the finned octopods, represent the oldest evolutionary lineage of the octopods (Voss, 1988). The cirrates are soft-bodied, semigelatinous animals with a pair of small to large fins, a deep and sometimes complicated web and a relatively large, single internal shell. They swim by medusoid action of the web, by jet propulsion, by beating the fins or by a combination of all three (Pereyra, 1965; Roper & Brundage, 1972). Although swimmers, they live just above the bottom and are rarely captured in the mid-depths.

The deep-sea benthic incirrates resemble, in general appearance, the typical shallow-water octopods. They are soft to firm bodied,

have a moderate to deep web and vestigial paired shell-remnants or stylets. They crawl about the bottom or swim by jet propulsion for short distances. While there are several families that have deep-sea pelagic octopods (see Thore, 1949), only the benthic species are considered here.

In both orders, the benthic and "near benthic" females produce large eggs resulting in young that, we suppose, take up the adult habitat and mode of life immediately after hatching from the egg.

One might expect that the genera and species of the deep-sea cirrates would have a much broader distribution than would the slower moving, bottom crawling deep-sea incirrates. Such, however, is not the case although our studies are limited by a paucity of specimens and much confusion concerning identifications.

TABLE 1. List of cirrate octopods arranged according to Voss (1988) with depth of capture and nomenclatural status.

Cirroteuthidae	
<i>Cirroteuthis muelleri</i>	Eschricht, 1836. 0–2342 m.
<i>Cirrothauma murrayi</i>	Chun, 1911. 1500–4500 m.
Stauroteuthidae	
<i>Stauroteuthis syrtensis</i>	Verrill, 1879. 457–2463 m.
Opisthoteuthidae	
<i>Grimpoteuthis megaptera</i>	(Verrill, 1885). 1929–4710 m
<i>Grimpoteuthis umbellata</i>	(Fischer, 1883). 1140–5274 m
<i>Grimpoteuthis pacifica</i>	(Hoyle, 1885). 4465 m.
<i>Grimpoteuthis meangensis</i>	(Hoyle, 1885). 915–1098 m.
<i>Grimpoteuthis caudani</i>	(Joubin, 1896). 650 m
	<i>Nomen dubium.</i>
<i>Grimpoteuthis plena</i>	(Verrill, 1885). 1964 m.
<i>Grimpoteuthis hippocrepium</i>	(Hoyle, 1904). 3336 m.
	<i>Nomen dubium.</i>
<i>Grimpoteuthis mawsoni</i>	(Berry, 1917). 527–549 m.
	<i>Nomen dubium.</i>
<i>Grimpoteuthis grimaldi</i>	(Joubin, 1903). 1804–1901 m.
	(= <i>Opisthoteuthis</i> ?)
<i>Grimpoteuthis wuelkeri</i>	(Grimpe, 1920). 2057 m.
	<i>Nomen dubium.</i>
<i>Grimpoteuthis albatrossi</i>	(Sasaki, 1920). 487–1680 m
<i>Grimpoteuthis glacialis</i>	(Robson, 1930). 500 m.
<i>Grimpoteuthis bruuni</i>	Voss, 1982. 250–360 m.
<i>Opisthoteuthis agassizi</i>	Verrill, 1883. 922–2250 m.
<i>Opisthoteuthis depressa</i>	Ijima & Ikeda, 1895.
	128–1074 m.
<i>Opisthoteuthis pluto</i>	Berry, 1918. 833 m
<i>Opisthoteuthis persephone</i>	Berry, 1918. 549 m.
<i>Opisthoteuthis medusoides</i>	Thiele, 1915. 399 m.
<i>Opisthoteuthis extensa</i>	Thiele, 1915. 769 m.
<i>Opisthoteuthis californiana</i>	Berry, 1949. 125–1100 m.
<i>Opisthoteuthis japonica</i>	Taki, 1962. 150 m.
<i>Opisthoteuthis philippi</i>	Oomen, 1976. 275–365 m
	<i>Uncertain status</i>
<i>Chunioteuthis ebersbachi</i>	(Grimpe, 1916). 1100 m.
<i>Chunioteuthis gilchristi</i>	(Robson, 1924). 2562 m.
<i>Froekenia clara</i>	Hoyle, 1904. 1016 m.
<i>Cirroteuthopsis massyae</i>	Grimpe, 1920. 1409 m.

CIRRATA

The Cirrata contains 29 species in 8 genera (Table 1). These are divided into three families based upon web and shell types: Cirroteuthidae, Stauroteuthidae and Opisthoteuthidae.

Cirroteuthidae

The cirroteuthids contain two monotypic genera represented by *Cirroteuthis muelleri* and *Cirrothauma murrayi*. All of the cirroteuthids are fragile, soft-bodied animals, especially *Cirroteuthis*. Meaningful measurements are exceedingly difficult to obtain from the specimens, and internal organs are relatively unstudied. Perhaps these genera will be found to be more speciose when sufficient specimens are available.

Cirroteuthis muelleri is known from the northwestern Atlantic (Voss, unpublished), Baffin Bay to Iceland (Eschricht, 1836; Voss, unpublished), off Jan Mayen (Appellöf, 1893) and from off Oregon (Voss & Percy, in preparation). These data suggest an amphiboreal distribution (Fig. 1). Although a number of species of fish show this amphiboreal distribution, most are separated into Atlantic and Pacific subspecies (Ekman, 1953). The apparent absence of a median pallial adductor in Atlantic specimens (Robson, 1932) is erroneous since examination of well-preserved WALTHER HERWIG specimens from the North Atlantic proved that this structure was present. No other characters have been found by which to separate the two populations. Because of the high northern occurrence in the Atlantic, the distribution could be continuous through the Arctic Ocean even though no high Arctic records are known. The species has been taken from the surface (off Greenland) to 2342 m.

Cirrothauma murrayi has been monographed by Aldred *et al.* (1983) who gave all known records. Additional records in Fig. 1 have been added from specimens in the University of Miami collections. This species is known from the coasts of Europe and northwestern Africa to off northeastern South America and along the eastern coast of North America from about New York to the Bahamas and questionably from the Indian Ocean. Its normal depth range is 1500 to 3000 m. One specimen was taken from an ice hole in the Arctic Ocean. If all specimens prove to belong to a single species, this species will be the only widely distributed, nearly cosmopolitan, species among the deep-water octopods.

Stauroteuthidae

Like the cirroteuthids, stauroteuthids are fragile, soft-bodied animals. This family is represented only by *Stauroteuthis syrtensis*. It occurs from Nova Scotia (Verrill, 1879) along the Atlantic coast of North America to north of the Bahamas (Voss, unpublished) (Fig. 1). Except for one questionable record, this species occurs only in the western North Atlantic. Its depth range is 457 to 2463 m.

Opisthoteuthidae

As now understood, this family includes the majority of the cirrates: 22 species belong to

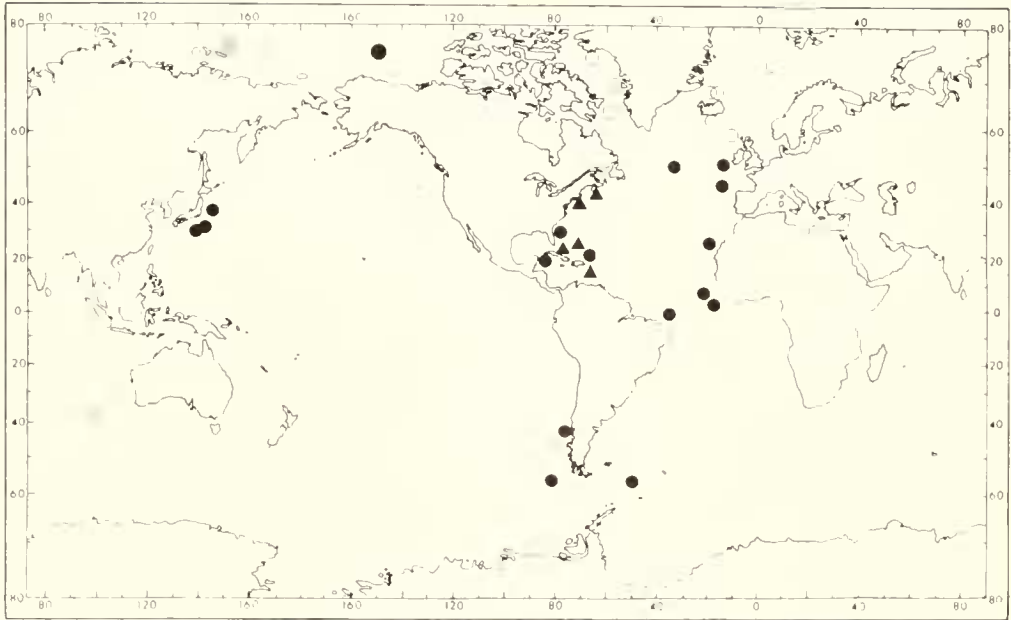


FIG. 1. Cirroteuthidae. ○ *Cirroteuthis muelleri*. ● *Cirrothauma murrayi*. Stauroteuthidae. ▲ *Stauroteuthis syrtensis*.

the two genera *Grimpoteuthis* and *Opisthoteuthis*.

The genus *Grimpoteuthis* occurs throughout the Atlantic and Pacific oceans and the Antarctic (Fig. 2), living in depths from about 200 m to below 7000 m (Robson, 1932). The identity of the majority of species is uncertain and many species are represented by single specimens. As a result, the geographical range of many species is not yet established. At present no species is known to be widespread.

Nine species have been described and three are in manuscript (Voss & Percy, in preparation; Voss, in preparation). Brief inspection of the GALATHEA collections suggests that this number may be doubled when these specimens are reported upon.

Grimpoteuthis glacialis is known from south of the Antarctic Convergence from South Georgia, the Palmer Peninsula and the Ross Sea (Robson, 1930; unpublished ELTANIN records, University of Miami). It probably occurs throughout the Southern Ocean south of the convergence. A second undescribed Southern Ocean species occurs in the Scotia Sea (WALTHER HERWIG specimens, Voss, in preparation). *Grimpoteuthis bruuni* occurs

off northern Chile and Peru (Voss, 1982). *G. umbellata*, the type species, is still relatively unknown but occurs off Mauritania and the Azores (Fischer, 1883; Robson, 1932). Several specimens identified as this species (Robson, 1932; personal observations) are questionable.

Verrill (1885) described *G. megaptera* and *G. plena* from off New England. The latter is a *nomen dubium*, but *G. megaptera*, with many misidentified specimens, may be widespread in the North Atlantic.

In the same year Hoyle (1885) described two species taken by the CHALLENGER: *G. pacifica* from near the Coral Sea and *G. meangensis* from north of the Celebes. No subsequent specimens identifiable to either of these two species have been reported. In 1904 Hoyle also described *G. hippocrepium* from off the Gulf of Panama. The validity of all three species is questionable because of the brief descriptions and poor illustrations.

Grimpoteuthis albatrossi was described by Sasaki (1920) from south of the Aleutians from specimens taken by the United States Fish Commission steamer ALBATROSS. It also occurs off Japan (Sasaki, 1929).

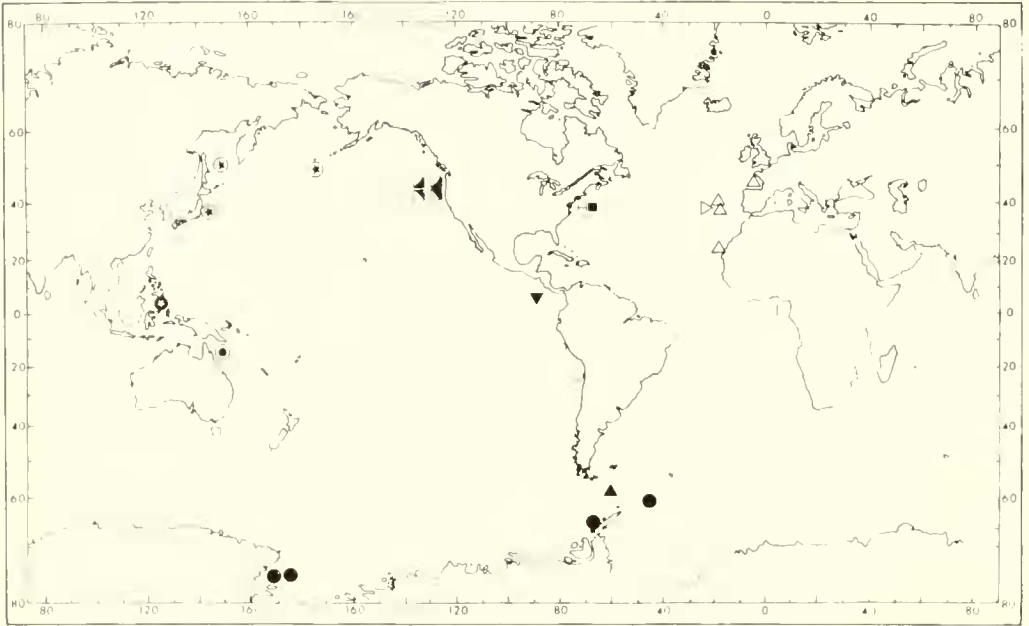


FIG. 2. Opisthoteuthidae. ○ *Grimptoteuthis bruuni*, ● *G. glacialis*, ▲ *G. sp. A*, ■ *G. sp. B*, ▽ *G. sp. C*, ⊙ *G. meangensis*, ● *G. pacifica*, △ *G. umbellata*, □ *G. megaptera*, ■ *G. plena*, ▼ *G. hippocrepium*, ▷ *G. grimaldi*, ⊙ *G. albatrossi*.

The beautifully illustrated and well described *G. grimaldi* Joubin, 1903, is a problem. Since its original description from off the Azores, additional specimens have been assigned to this species in the literature (Joubin, 1920; Bruun, 1945). My study of the optic lobe of cirrates (unpublished) indicates, however, that *G. grimaldi* is probably an *Opisthoteuthis* and may even be *O. agassizi*.

The genus *Opisthoteuthis* occurs in moderate depths, mostly between 100 and 1000 m in tropical and temperate seas (Fig. 3). It ranges from about 50°N to 45°S. Only three species have been taken in depths greater than 1000 m; the deepest record is 2250 m (Verrill, 1885).

If identifications are correct, *Opisthoteuthis agassizi* occurs in the eastern Atlantic from southwest of Ireland (Chun, 1913) to off Spain, and the western Mediterranean (Morales, 1959), the Gulf of Guinea (Voss, in preparation) and south to off southwest Africa (Adam, 1962). Its distribution in the W Atlantic appears to be more limited, ranging from northeast of the Bahamas (Univ. of Miami collections) and Gulf of Mexico (Voss, 1956) to northeastern Brazil (Univ. of Miami collections).

Opisthoteuthis californiana occurs in northern California (Berry, 1949) and Washington (Pereyra, 1965) waters and has since been reported by Taki (1963) from off Honshu. Two other species, *O. depressa* and *O. japonica*, also occur in Japanese waters.

Thiele (1915a) described *O. extensa* from a VALDIVIA station southwest of Sumatra and *O. medusoides* from off Zanzibar. In 1918 Berry described *O. persephone* and *pluto* from captures by the ENDEAVOUR in the Great Australian Bight. Many more specimens of the latter two species have since been taken. Both apparently are limited to Australian waters.

The last species described is *Opisthoteuthis philippi* from off southwest India (Oomen, 1976).

The paucity of records prevents generalizations on the biogeography of the individual species.

INCIRRATA

The incirrate deep-sea octopods contain 48 species distributed unevenly in 11 genera (Ta-

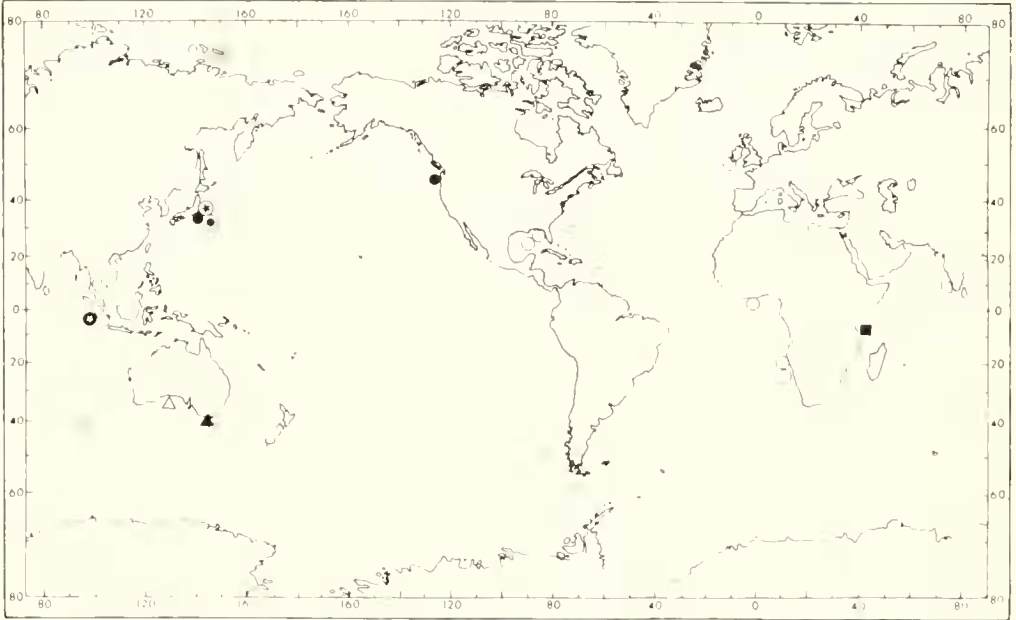


FIG. 3. Opisthoteuthidae. ○ *Opisthoteuthis agassizi*, ⊙ *O. depressa*, ⊕ *O. extensa*, ■ *O. medusoides*, ⊕ *O. japonica*, ● *O. californiana*, □ *O. philippi*, △ *O. pluto*, ▲ *O. persephone*.

ble 2). I have recently (Voss, 1988) grouped these in three subfamilies: Bathypolypodinae, Pareledoninae and Graneledoninae. In general, the deep-sea incirrates do not occupy as great depths as do the cirrates, ranging from about 200 m to nearly 4000 m but with many living to about 500 m. All, however, show modifications to reflect a deep-sea habitat.

Robson's (1932) classification of the incirrates, in my opinion, cannot be maintained. Some major shifts are made here, based partly on the number of longitudinal sucker rows and the presence or absence of an ink sac and crop.

Bathypolypodinae

This subfamily contains three genera, *Bathypolypus*, *Teretoctopus* and *Benthoctopus*. All have biserial arm suckers and no ink sac.

Bathypolypus contains five species of which three are found in the North Atlantic (Mangold-Wirz, 1963; Toll, 1985), one off Japan (Sasaki, 1929) and one in the Indian Ocean (Thiele, 1915b) (Fig. 4). *B. arcticus* is found in the North Atlantic from the Straits of Florida (in deep water) north to Baffin Bay,

Denmark Straits, Iceland, northern Great Britain and the North Sea to Spitzbergen and the Arctic Ocean north of European Russia (Nesis, 1982; Kumpf, 1958). It appears to be an Atlantic Boreal and Arctic species. *B. arcticus* is also confused with *B. faeroensis*, recently reinstated by Toll (1985), and *B. proschi* Muus, 1962. Further work may show that true *B. arcticus* may have a more limited distribution.

B. sponsalis occurs along the Atlantic Spanish coast southward to Senegal (Adam, 1960) and the Cape Verde Islands (Fischer & Fischer, 1892) and the western Mediterranean Basin (Wirz, 1955; Morales, 1958) in depths from 400 to 930 m. Its distribution reflects the typical Mauritanian—Lusitanian—Mediterranean pattern (Ekman, 1953: 80).

B. salebrosus is found off northern Honshu, the Kurile Islands and in the Okhotsk Sea (Sasaki, 1929). It lives between about 450 and 800 m.

B. valdiviae is distributed from near Durban, South Africa, to off Walfisch Bay, Namibia, in depths from 400 to 800 m (Thiele, 1915b; Sanchez & Moli, 1984). Its range encompasses the Cape Province and the Namaquan Province, both dominated by the

TABLE 2. List of incirrate octopods arranged according to Voss (1988) with depths of capture and nomenclatural status.

Bathypolypodinae	
<i>Bathypolypus arcticus</i> (Prosch, 1849)	To 1543 m.
<i>Bathypolypus sponsalis</i> (P. & H. Fischer, 1892)	930–1250 m.
<i>Bathypolypus faeroensis</i> (Russell, 1909)	480–1030 m.
<i>Bathypolypus valdiviae</i> (Thiele, 1915)	403–860 m.
<i>Bathypolypus salebrosus</i> (Sasaki, 1920)	487–805 m.
<i>Bathypolypus proschi</i> Muus, 1962	<i>Nomen dubium</i>
<i>Teretoctopus indicus</i> Robson, 1932	996 m.
<i>Teretoctopus alcocki</i> Robson, 1932	353–1281 m.
<i>Benthoctopus piscatorum</i> Verrill, 1879	220–2492 m.
<i>Benthoctopus levis</i> (Hoyle, 1885)	13–137 m.
<i>Benthoctopus januari</i> (Hoyle, 1885)	350–732 m.
<i>Benthoctopus ergasticus</i> (P. & H. Fischer, 1892)	470–915 m.
<i>Benthoctopus lotheri</i> (Chun, 1914)	1365 m.
<i>Benthoctopus hokkaidensis</i> (Berry, 1921)	487–920 m.
<i>Benthoctopus abruptus</i> (Sasaki, 1920)	1074 m.
<i>Benthoctopus pseudonymus</i> (Grimpe, 1922)	1599 m.
<i>Benthoctopus berryi</i> (Robson, 1924)	2196 m.
<i>Benthoctopus eureka</i> (Robson, 1929)	Depth unknown.
<i>Benthoctopus sibircus</i> Loning, 1930	Stomach of walrus
	<i>Nomen dubium</i>
<i>Benthoctopus thielei</i> Robson, 1932	On shore
<i>Benthoctopus profundorum</i> Robson, 1932	741–3431 m.
<i>Benthoctopus magellanicus</i> Robson, 1932	145 m.
<i>Benthoctopus oregonae</i> Toll, 1981	640–1080 m.
Pareledoninae	
<i>Pareledone charcoti</i> (Joubin, 1905)	18–595 m.
<i>Pareledone turqueti</i> (Joubin, 1905)	25–1116 m.
<i>Pareledone hamsoni</i> (Berry, 1917)	494–655 m.
	<i>Nomen dubium</i>
<i>Pareledone adeliana</i> (Berry, 1917)	527–549 m.
	<i>Nomen dubium</i>
<i>Pareledone polymorpha</i> (Robson, 1930)	15–1116 m.
<i>Velodona togata togata</i> Chun, 1915	748 m.
<i>Velodona togata capensis</i> Robson, 1929	402–457 m.
<i>Vosseledone charrua</i> Palacios, 1978	10–200 m.
<i>Tetracheledone spinicirrus</i> Voss, 1955	183–544 m.
<i>Eledone moschata</i> (Lamarck, 1798)	Above 300 m.
<i>Eledone cirrhosa</i> (Lamarck, 1798)	10–800 m.
<i>Eledone caparti</i> Adam, 1950	60–170 m.
<i>Eledone thysanophora</i> Voss, 1962	Tide pool.
<i>Eledone massyae</i> Voss, 1964	60–170 m.
Graneledoninae	
<i>Graneledone verrucosa</i> (Verrill, 1881)	852–2297 m.
<i>Graneledone challengerii</i> (Berry, 1961)	1153–1867 m.
<i>Graneledone verrucosa media</i> (Joubin, 1918)	1458 m.
	<i>Nomen dubium</i>
<i>Graneledone antarctica</i> Voss, 1976	2341 m.
<i>Graneledone macrotyla</i> Voss, 1976	1647–2044 m.
<i>Graneledone boreopacifica</i> Nesis, 1982	1165–1500 m.
<i>Thaumeledone brevis</i> (Hoyle, 1885)	800–3931 m.
<i>Thaumeledone gunteri</i> Robson, 1930	410 m.
<i>Bentheledone rotunda</i> (Hoyle, 1885)	3596 m.
<i>Bentheledone albida</i> (Berry, 1917)	3111 m.

Agulhas Current, which probably is responsible for this distribution.

The genus *Teretoctopus* contains only two species, *T. indicus* and *T. alcocki*. *T. indicus* has been reported from the pearl grounds off Ceylon (Robson, 1932) and the upper Arabian Sea in 1000 m (Massy, 1916b). *T. alcocki* is known from the Bay of Bengal and

the Andaman Sea to the upper Arabian Sea (Robson, 1932) between 500 and 1281 m. Little is known of these two Indian Ocean species other than Robson's (1932) comments.

The genus *Benthoctopus* occurs from the Arctic Ocean to the Southern Ocean (Fig. 5). Specific identifications are difficult; there are numerous synonyms and the literature is filled with misidentifications. All of the 15 or so species have somewhat limited ranges. They live from about 200 m to in excess of 3000 m.

Benthoctopus piscatorum is an Atlantic Boreal species found from New England to the British Isles, North Sea and off Norway (Robson, 1932). It may also be found in the High Arctic and around Spitsbergen (Robson, 1932) but its northern and eastern ranges are not known. *B. ergasticus* is in the Eastern Atlantic southwest of Ireland (Massy, 1909) and the Mauritanian upwelling area (Fischer & Fischer, 1892). *B. januari* is strictly Atlantic, distributed from the Gulf of Mexico (Voss, 1956) to middle Brazil (Hoyle, 1886). Toll (1981) described *B. oregonae* from the middle of the former's range.

The only other species with sufficient information to permit speculation on its range is *B. magellanicus* from the Valdés Peninsula, Argentina (Ré, personal communication) to Tierra del Fuego (Robson, 1932) and apparently N to Chiloe Island (Voss, unpublished).

Greater deep-trawling efforts will certainly reveal more species and wider distributions. There are four species off Japan and Voss & Percy (in preparation) have four new species from off Oregon. But records are few and scattered widely. Surprisingly, few are known from the Southern Ocean.

Pareledoninae

This subfamily contains the deep-sea genera *Pareledone*, *Velodona*, *Tetracheledone* and the closely related shallow-water genus *Vosseledone* and the more distantly related genus *Eledone*. *Eledone* is retained only provisionally in this subfamily as it shares the common characters of uniserial arm suckers, an ink sac and a crop. However, Robson (1932) and others have held that it is not truly related to the other members of the subfamily.

The species of *Pareledone* are all from the Southern Ocean (Fig. 6), living primarily south of the Antarctic Convergence (Robson, 1932; Dell, 1959; Taki, 1961; Voss, in preparation) although *P. turqueti* was recorded off Pará,

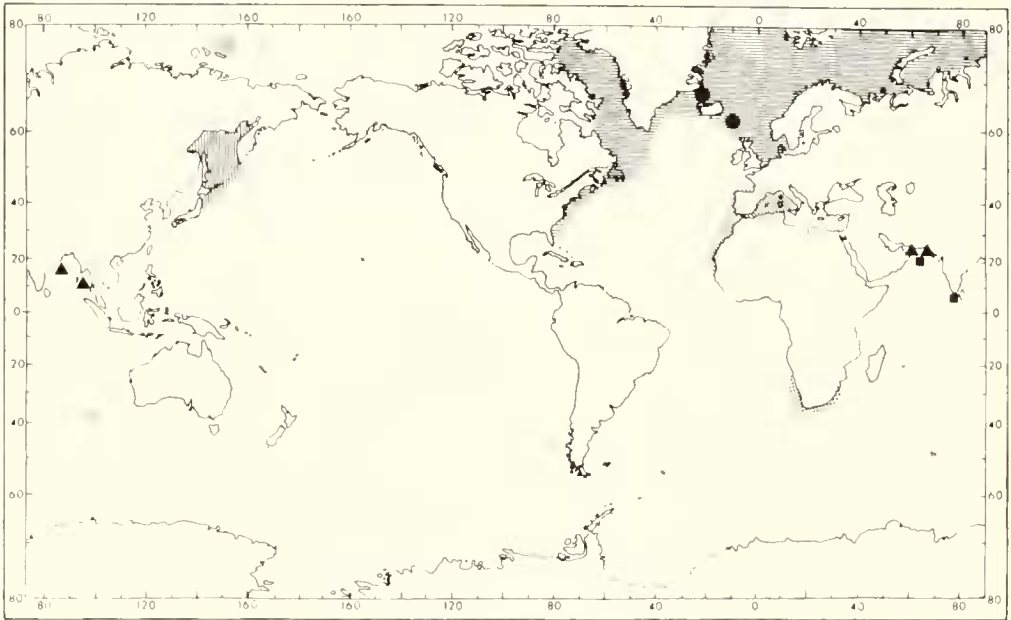


FIG. 4. Bathypolypodinae. ▨ *Bathypolypus arcticus*, ▩ *B. sponsalis*, ▧ *B. salebrosus*, ▦ *B. valdiviae*, ● *B. faeroensis*, ■ *Teretoctopus indicus*, ▲ *T. alcocki*.

Brazil, by Massy (1916a) from deep trawling of the TERRA NOVA expedition. It was also taken in Antarctic Deep Water. All of the species are circumpolar, living from tide pools in the Ross Sea to below 2000 m, with temperature apparently the controlling factor (Voss, in preparation).

Velodona togata has been taken twice from off Zanzibar (Chun, 1915; Voss, unpublished). A subspecies, *capensis*, occurs in the Cape Province (Robson, 1932). This species is probably widely distributed along the East African coast in depths between 400 m and 800 m (British Museum collections). *Vosseledone charrua* has a similar distribution along the eastern coast of South America in shallow water, only 10 m to 200 m (Palacio, 1978), but it is closely related to the deep-sea *Pareledone* in many of its features. *Tetracheledone spinicirrus* is known only from north Florida to the Gulf of Mexico and the northern Caribbean in 183 to 544 m (Voss, 1956). *Vosseledone*, *Velodona* and *Tetracheledone*, while occurring in shallow to moderate depths, in all other respects are deep-water animals closely resembling the genus *Graneledone* to which, on superficial examination, many of them would seem to belong.

Eledone was originally thought to be Mediterranean with only two species, *cirrosa* and *moschata*. Later a West African species, *E. caparti*, was described (Adam, 1950) from the Guinean Province. More recently another species, *E. massyae*, was added from off Brazil (Voss, 1964) where an additional, undescribed species occurs (Haimovici, in preparation), and finally one from southwest Africa, *E. thysanophora*, was described (Voss, 1962). A new species from Australia has recently been found (Lu, personal communication). Apparently the genus is circumpolar and warm temperate in distribution (Fig. 7). It is found in moderate depths, mostly above 300 m with a single record to 800 m. Its true position and relationship with both the deep-water and shallow-water genera has yet to be solved.

Graneledoninae

This subfamily contains the genera *Graneledone*, *Thaumeledone* and *Bentheledone* (Fig. 8). They are all deep dwellers, living between 1000 m to in excess of 3500 m. The genus *Graneledone* shows a somewhat

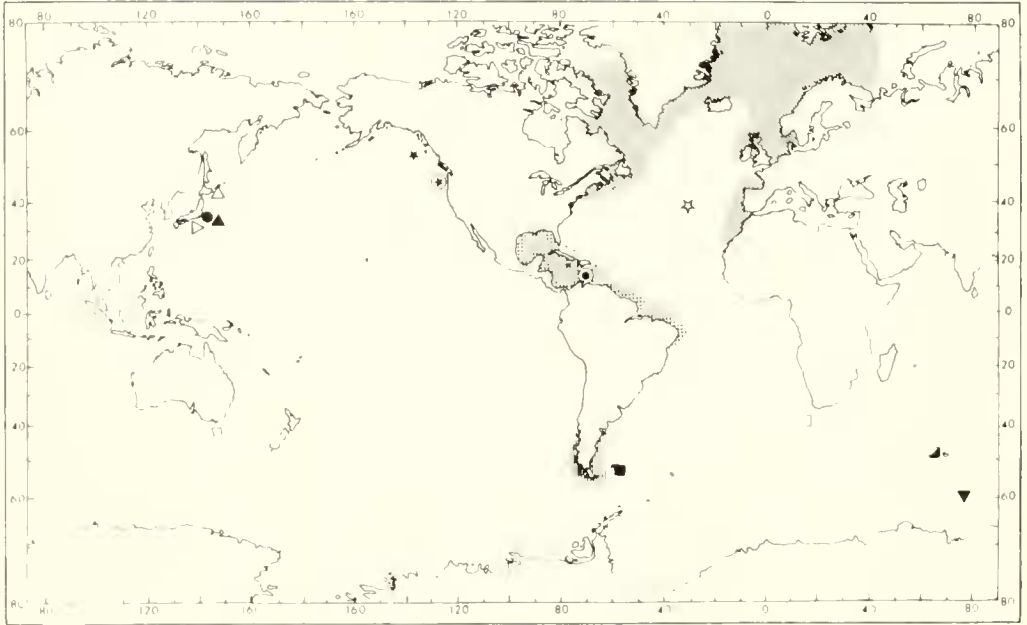


FIG. 5. Bathypolypodinae. ▨ *Benthoctopus piscatorum*, ▧ *B. ergasticus*, ▩ *B. magellanicus*, ▪ *B. januari*, ● *B. oregonae*, ■ *B. eureka*, □ *B. berryi*, ☆ *B. pseudonymus*, ▲ *B. fuscus*, △ *B. hokkaidensis*, ▷ *B. abruptus*, ● *B. profundorum*, ▼ *B. levis*, ◼ *B. thielei*, ★ *B. sp. A*, ☆ *B. spp. A, B, C, D*.

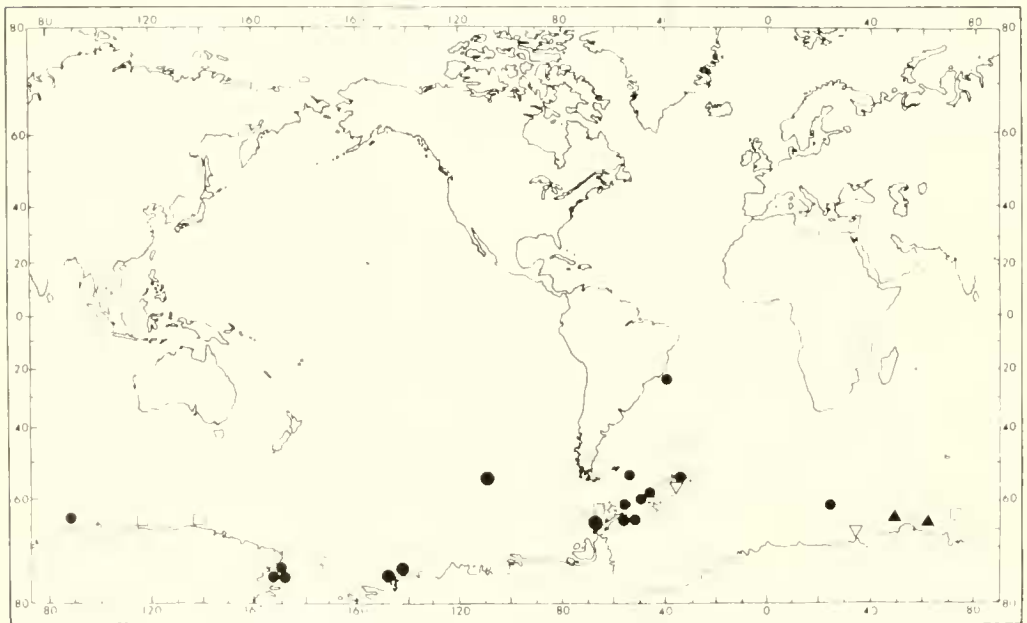


FIG. 6. Pareledoninae. ○ *Pareledone polymorpha*, ● *P. turqueti*, ▽ *P. senoi*, ▲ *P. harrisoni*, □ *P. charcoti*.



FIG. 7. Pareledoninae. ○ *Velodona togata*, ● *Vosseledone charrua*, ▼ *Tetracheledone spinicirrus*, □ *Eledone massyae*, ▲ *E. nigra*, △ *E. thysanophora*, ▨ *E. cirrosa*, ▩ *E. moschata*, ▤ *E. caparti*.

bipolar distribution with *G. verrucosa*, *G. boreo-pacifica* and *G. sp. A* (the latter two perhaps identical), in N waters (Voss & Percy, in preparation), and *G. antarctica*, *G. macrotyla* and *G. challengerii* (Voss, unpublished) in the Southern Ocean and north of New Zealand. An unidentified specimen, examined by me from off the Gulf of Panama, may represent an additional species (sp. B).

The genus *Thaumeledone* contains two nominal species, *T. brevis* and *T. gunteri*. Unpublished records of *T. brevis* show that it is distributed from the Palmer Peninsula to the Ross Sea and is probably circumpolar south of the Antarctic Convergence. *T. gunteri* is probably a synonym and was reported from off South Georgia. It was taken in 410 m (Robson, 1930) while *T. brevis* lives between 800 m and 3931 m (Robson, 1932; Voss, unpublished).

Bentheledone consists of two described species, *B. rotunda*, and *B. albida*, with two undescribed species (Voss, in preparation). All occur south of the Antarctic Convergence in depths from 3000 m to 3596 m. They are probably circumpolar. Despite the extensive trawling effort in the Southern Ocean, no specimens of *Bentheledone* have been taken from moderate depths.

DISCUSSION

Unfortunately the systematics of the deep-sea octopods, and in particular the cirrates, have been sadly neglected. Robson's (1932) monographic study of the cirrates was the last attempt to make order out of the group. It did not succeed, partly because of Robson's mental decline and partly because of the poor quality and quantity of available collections. The situation has not altered appreciably since then because, while considerable additional material has accumulated, the existing types have deteriorated to such an extent that reliance must be given to the original, often inadequate, descriptions. The next few years, however, should show progress in cirrate systematics and biogeography as a result of study of the collections made by the USNS ELTANIN in the Antarctic and the Danish GALATHEA on her round-the-world, deep-trawling expedition, all now at Miami.

Among the cirrates, several distributional patterns are evident, even at this time. *Cirrothauma* is found in both the Atlantic and Pacific Oceans. *Stauroteuthis* is known definitely only from the western North Atlantic, including the Caribbean Sea.

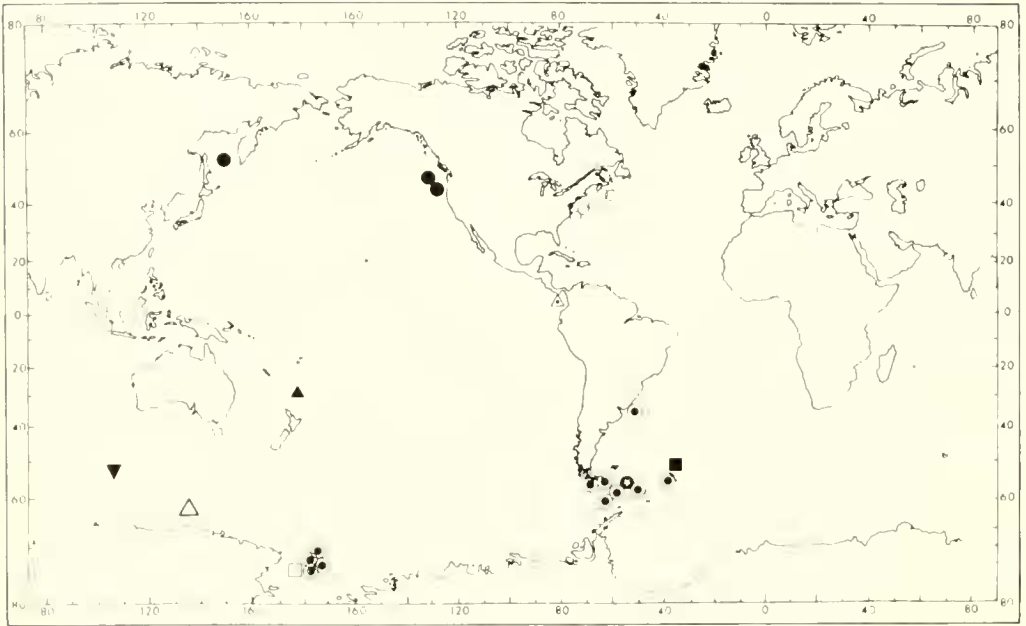


FIG. 8. Graneledoninae. ○ *Graneledone verrucosa*, ● *G. sp. A*, ▲ *G. challengeri*, △ *G. sp. B*, □ *G. antarctica*, ⊙ *G. macrotyla*, ⊖ *Thameledone brevis*, ■ *T. gunteri*, ▼ *Benthedone rotunda*, ▽ *B. albida*.

Grimpoteuthis is widely distributed but does not occur in the Arctic, living no further north than about 50°N. It is the only genus of cirrates that has representatives in the Southern Ocean south of the Antarctic Convergence.

Opisthoteuthis is known only from 45°N to 45°S. Living in shallower depths, its distribution reflects the shallow-water hydrographic regimes.

The Incirrata have fared little better. Again Robson (1932) brought together all of the known information on the group but it is a hodge-podge of misidentification by previous authors and reflects a lack of comparative morphological data. Many of the species described both before and after Robson were done without referring to the types, and since 1932 are based upon Robson's confused decisions. Again, many of the types are in poor condition or are immature specimens lacking important specific characters (Voss, in preparation).

The Bathypolypodinae contains primarily northern hemisphere genera and species. Five of the six species of *Bathypolypus* occur from about 20°N to the Atlantic and Pacific Subarctic with one extending to Spitsbergen.

The sole southern exception is *B. valdiviae*, which is found off South Africa in the Agulhas Current or the southern end of the cold Benguela Current. *Teretioctopus* is limited to the deep underlying cold water of the tropical Indian Ocean.

Benthoctopus is the most widely distributed of the Bathypolypodinae but only four of the nineteen species are found in the southern hemisphere with two south of the Antarctic Convergence. Of the remaining 15 species, one is widely distributed in the North Atlantic Boreal to the Subarctic and perhaps to the High Arctic. Two are tropical and nine are northern temperate.

The Pareledoninae comprises two groups showing distinctly different distributional patterns. *Pareledone* is strictly Southern Ocean; all of the known species have their main concentrations south of the Antarctic Convergence and are circumpolar. The few catches north of the convergence, one off Montevideo and the others near the Falkland Islands, were in cold Antarctic Deep Water.

The remaining genera of the Pareledoninae are all Atlantic and Indian Ocean in occurrence. Their distribution reflects the general surface hydrographic regimes and all have

restricted distributions, reflecting their moderate-depth, continental slope habitats.

The Graneledoninae are in the western North and South Atlantic, Pacific and Southern Ocean. *Graneledone* has a somewhat bipolar distribution with two species in the colder North Atlantic and North Pacific Subarctic Water and three in Southern Ocean. However, one species occurs north of New Zealand and one off the Gulf of Panama, both in deep water.

The genera *Thaumeledone* and *Bentheledone* contain the deepest dwelling of all the Incirrata and are found in the Southern Ocean south of the Antarctic Convergence with only one record in Antarctic Deep Water off Argentina.

Of the 77 species of deep-water octopods, 25 percent are confined to the Southern Ocean in Antarctic Water; 22 percent are limited to Atlantic and Pacific Subarctic Water. Ten percent may be considered shallow to moderate depth inhabitants of the warm water regions of the world. The remaining 43 percent occupy the great depths below the tropical and warm temperate regions of the world, living in cold deep water derived from either the Antarctic or the Arctic Deep or Intermediate Water.

The high percentages of species occurring in the Southern Ocean is probably due to the high productivity of the waters between the Antarctic Convergence and the Antarctic continent, with somewhat lower levels northward to the Subtropical Convergence. The same situation is found with regard to the species in the North Atlantic and North Pacific in Subarctic Water. The dearth of species in the Arctic Ocean may well correlate with the lower productivity of the Arctic Ocean in general. If one compares the distributions of the deep-water octopods in the world oceans with the map of ocean productivity as depicted by Ebeling (1962), one finds a high correlation with species richness and high productivity (above 100-200 gC/m²/year) with few genera and species in less productive waters.

ACKNOWLEDGEMENTS

N. A. Voss read the manuscript critically and offered many suggestions. I have benefited from the study of numerous specimens in many museums in this country and Europe, too numerous to mention here but to whom thanks are extended. This paper is a scientific

contribution from the Rosenstiel School of Marine and Atmospheric Science, University of Miami.

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